

## THE ZOOGEOGRAPHY OF MARSUPIALS,

WITH NOTES ON THE ORIGIN OF THE AUSTRALIAN FAUNA.

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NOTWITHSTANDING the wealth of literature on the subject, the problem of the origin of our Australian marsupial fauna is still a fascinating field for research. It is almost with trepidation that the writer enters this arena of controversy, wherein so many able authorities have expressed diverse views. None the less, it seems desirable to try and focus the results of some of our more recently acquired knowledge, together with a purview of the work of the past, so far as space and opportunity permit.

For the sake of consecutiveness it is necessary to set out, by means of extracts, some of the views of authorities. In 1893 H. O. Forbes published a formidable list of vertebrates (the majority being birds), invertebrates, and plants chiefly confined to the southern hemisphere suggesting affinities between South America, Australia, various Pacific Islands, and South Africa, from which he deduced the existence of a former circumpolar continent. When analysed to-day, however, many of the examples quoted by Forbes, with reference to Australia and South America, have lost their significance, and any affinities that remain do not afford evidence of lineal relationships requiring southern Tertiary land bridges.

In 1892 Baldwin Spencer accepted the north-western origin in pre-Cretaceous time of the monotremes and the primitive polyprotodont fauna (p. 116), spreading south and then east. Later, in his valuable summary of the results of the Horn Expedition (1896), Spencer considered that the northern origin of marsupials was practically negated by the feeble development of the more primitive polyprotodonts in north-eastern Australia (p. 185), although he believed that the characteristic Diprotodonts had mainly developed there. He considered that Papua was the last and not the first land of the Australian region to be reached by the marsupial fauna.

Haswell (1914), in his interesting review of the Australian fauna, considers (p. 217) the connection between Australia and South America "at some time antecedent to the Pliocene" to be clearly established.

In several papers (1893, 1895, 1899, and 1912) Hedley has argued for the Antarctic origin of our most characteristic fauna, and his advocacy carries weight.

Hedley (1899) wrote of "a rich fauna of Antarctic origin, which, entering by Tasmania, overran the whole continent, crossed Torres Strait into New

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NOTE—The substance of this paper was given before the Zoology Section of the Pan-Pacific Conference in Sydney, August, 1923.

Guinea, and reached its utmost eastern limit in the Solomons. Characteristic members of it are the marsupials, monotremes, cystignathous frogs, venomous snakes, and snails of the Order Macroogna." Using Tate's term, he calls this the Euronotian element, and claims it as the most characteristic fauna. In his address to the Linnean Society of London in 1912, Hedley states: "In Australia marsupials and monotremes are least developed in the North; proceeding southward more groups successively appear till ultimately Tasmania has, as Professor Spencer expressed it, 'a condensation of most, that is noteworthy in the Australian Region.'" This aspect of the Antarctic theory appears to the writer to be open to adverse criticism. It is advisable to analyse first living species of Polyprotodontia.

**Dasyuridæ.**—The supposed paucity of polyprotodont forms in Papua and north-eastern Queensland must be examined in the light of recent work, which has greatly increased our knowledge of the range of present-day and fossil marsupials. In this "Papuan" (Hedley) or "Torresian" (Spencer) sub-region, we find *Dasyurus maculatus*, *geoffroyi*, *gracilis*, *hallucatus*, *albopunctatus*, and *dæmonellus* (Thomas, 1904), the last two species being Papuan, and there is a doubtful record of *viverrinus* for Queensland in our State Museum. The known species are found to be very strongly represented in north-eastern Australia. In the genus *Phascogale* we find that the following species (subspecies omitted), have been described from the Torresian region during the last twenty years or so:—*lorentzii*, *nouhuou*, *naso* (three species from Dutch Papua, described by Jentink in 1911), *murex* O. Thos., 1913 (Papua), *melanura* O. Thos., 1912 (Papua); *bella* O. Thos., 1904, *minulus* O. Thos., 1906, and *ingrami*, O. Thos., 1906, are Northern Territory species; *godmani* O. Thos., 1923, comes from North Queensland. When these records are added to previous ones, the great majority of species of *Phascogale* are seen to be in the northern region. It is somewhat surprising to find that the known distribution of the allied genus *Sminthopsis* has been much more restricted, although the majority of the species now described are found in the northern region, and *S. rufigenis* was recorded for the Aru Islands in 1922 by Oldfield Thomas. When genera and species are considered, taking fossil as well as present-day forms, it is found that, instead of the polyprotodont marsupials being feebly developed in the northern region, it is there that they are most strongly represented.

In the opinion of Bensley (1903) and of Gregory (1920, p. 159), *Myrmecobius* is a specialised dasyurid. Wood Jones (1923, p. 126) has remarked that it is greatly handicapped by its habits: "It does not excavate deep burrows, it does not climb, it is not fleet of foot." The gradual restriction of its range in recent years suggests a far wider distribution in the past.

**Peramelidæ.**—During recent years we have added greatly to our knowledge of the Peramelidæ. In 1909 Allen and Barbour (*loc. cit.*) described the new genus *Suillomeles* for a species (*hispidus*) from Dutch Papua. In 1920 the genus *Rhynchomeles* was established by Oldfield Thomas for a species (*prattorum*) found

in Ceram. The genera *Echymipera* and *Peroryctes*, now separated from *Perameles* and *Isodon*, are distinctively Papuan. The writer has no knowledge of the characters of *Anuromeles*, Heller (1897), from Papua.

In 1903 Bensley pointed out that "Of the Peramelidæ all the species representing prototypal forms are Papuan" (p. 204). In 1923, with the addition of new genera and species the range and diversity of the Peramelidæ are far more significant. It now appears to be definitely established that the radiation of the Australian forms emanated from Papua, *Thylacomys* and *Chæropus* being specialised offshoots.

The discovery of new northern genera of peramelids is also of special interest in view of Osgood's opinion that this family exhibits characters suggestive of the incipient stages leading from polyprotodont to diprotodont groups. This is strengthened by their common syndactylism.

Osgood also states (1922, p. 135) that "the conclusion is unavoidable that among living forms those most suggestive of what the ancestor of *Cœnolestes* and other diprotodonts was like, are the Peramelidæ."

T. Thomson Flynn's recent work on the placenta in *Perameles* (1923), in which the genus is stated to be "a most primitive form" in this respect (p. 173), must be noted here.

**Notoryctidæ.**—The description of *Notoryctes caurinus*, by Oldfield Thomas in 1920, from Wollal, North-west Australia, makes an interesting northern extension of this curious marsupial, which is evidently a "specialised dasyurid."

**Diprotodontia.**—It is of interest to note a few of the more recent records for existing diprotodont marsupials. Taking the *Phalangeridæ* first, we find that no less than twelve out of twenty species of *Pseudochirus* occur in Papua, whilst the remaining Australian species are so richly represented in the north that the dominance of the genus there is undoubted. *Dactylopsila* (with eight species), *Dactylonax* and *Distœchurus* are distinctly Papuan genera, whilst *Acrobates*, *Petaurus*, *Eudromicia* (Mjöberg, 1915), and *Dromicia* are represented. *Phalanger*, including *Ceonix* and *Wyulda* (Alexander, 1918) has a remarkable distribution, ranging from Celebes to San Christoval in the Solomon Islands, from Talaut through the Moluccas, Timor, Papua, and New Britain, the Arus to North Queensland and North-west Australia, with twelve species. This wide-spread distribution affords striking evidence of northern marsupial extension, especially in view of the fact, mentioned by Guppy (1887), that cuscus are preyed upon by dogs which attack them when they descend at nightfall. The genera of the *Phalangeridæ* are thus seen to be overwhelmingly represented in northern regions.

Of the macropods, *Dendrolagus*, *Dorcopsis*, and *Dorcopsulus* are obviously Papuan. *Hypsiprymnodon*, an annectant type, is confined to North Queensland. The genera *Petrogale*, *Lagorchestes*, *Epyprymnus*, and *Onychogale* are represented in the northern State. *Macropus* has a still wider range to Papua, New Britain,

and the Aru Islands, but it seems clear that the evolution of the characteristic saltatorial forms, represented by this genus, has taken place mainly in the plains and forests of the Australian mainland. But, as in other families, the majority of the macropodian genera are to be found in the Torresian region.

When fossil representatives are considered, species of *Phascolomys* are more numerously represented in northern than in southern Australia.

**Tasmanian Fauna.**—With the possible exception of *Wynyardia bassiana* Spencer, dealt with elsewhere, the marsupial fauna of Tasmania presents no species, neither living nor fossil, that cannot be readily conceived as derivable from mainland forms. With the palæontological evidence for *Sarcophilus* and *Thylacinus* in Queensland, this is surely clear. In the list published by Clive E. Lord in 1918, twenty species are mentioned. Of these, one, *Petaurus breviceps*, is an artificial introduction from the mainland; there are three varieties of mainland forms (*Trichosurus vulpecula* var. *fuliginosus*, *Macropus ruficollis* var. *bennetti* and *M. giganteus* var. *fuliginosus*); no less than ten are found on the mainland (*Sminthopsis leucopus*, *Phascogale swainsoni*, *Dasyurus viverrinus*, *D. maculatus*, *Perameles gunni*, *P. obesula*, *Petaurus breviceps*, *Dromicia nana*, *Potorous tridactylus*, and *Macropus billardieri*); the remaining seven are confined to Tasmania (*Phascogale minima*, *Sarcophilus ursinus*, *Thylacinus cynocephalus*, *Phascolomys ursinus*, *Pseudochirus "cooki,"* *Dromicia lepida*, and *Bettongia cuniculus*). The present evidence of the marsupial fauna of Tasmania is decidedly in favour of the northern and not the southern origin of the group.

**Syndactylism.**—In 1923 Wood Jones analysed the relative age values of dental and pedal characters in classifying marsupials. After pointing out that the primitive marsupials were undoubtedly polyprotodont and didactylous, he shows that syndactylism must be a more primitive feature than diprotodontism because it is common to both groups; from a polyprotodont stock a syndactylous section arose which split up into the diprotodont group of herbivorous marsupials, on the one hand, and into the polyprotodont peramelids, on the other, the still more primitive didactylous dasyurids remaining unchanged. As it seems most improbable that this distinctive syndactylism could have been independently acquired, it is almost certain that this pedal character is one of greater antiquity than the specialised development of two front lower incisors, so characteristic of our dominant group. Syndactylism is thus a distinctive character of Australian marsupials, and it has apparently been developed here. It is absent in *Cænolestes* and in all other American marsupials, although in *Marmosa pusilla*, figured by Bensley (Plate VII, fig. 7), there is "an indication of the syndactylous condition of the Phalangeridæ" (p. 191). It is very doubtful, however, whether this approximation of the second and third digits in some species of *Marmosa* can be compared with the well-marked and dominant syndactylism of Australian groups. It is remarkable that in the illustration of *Marmosa pusilla* given by Oldfield Thomas (Pl. XXVIII, fig. 1) there is no trace of syndactylism. In specimens of *Marmosa mitis* (O. Bangs, 1898) in the Queensland Museum, examined by the writer, there is no evidence

of syndactylism, which does not appear to be even a specific character in the genus. The *M. pusilla* of the British Museum Catalogue is apparently referable to the nearly-allied *M. marica* O. Thomas, 1898.

**Fossil Marsupials.**—In tabulating evidence as to the origin of our marsupials, it is obvious that the index afforded by fossil genera and species is of even greater value than that of existing representatives. It appears to be an outstanding fact that *our fossil marsupial fauna is much more distinctively Australian than that of to-day*. We have ample evidence of gigantic specialised marsupials, such as *Diprotodon*, *Nototherium*, *Euryzygoma*, *Phascolonus*, *Sthenurus*, *Palorchestes*, *Procoptodon*, and *Thylacoleo*. There is no evidence whatever for the derivation of these specialised genera from either living or fossil American forms.

It is also very obvious that the genera existing to-day were much more richly represented in the past. The numerous species of *Macropus* (*sensu lato*) included very large forms, such as *M. anak*, whose trenchant premolar relatively dwarfs that of the Papuan *Dorcopsis*. The wombats of to-day are but a few survivors compared with their Pleistocene predecessors, which ranged from Clermont (Longman, 1917) to Western Australia. The carnivorous extinct *Thylacoleo carnifex* had for associates in Queensland species of *Sarcophilus* and *Thylacinus*, which were larger than Tasmanian species of to-day. A mandibular fragment of *Sarcophilus* was recorded from Rockhampton by the writer in 1921, this being an addition to the many records of the Queensland "devil" on the Darling Downs. The same species has been noted for Western Australia by L. Glauert, who has also recorded the following genera from his field:—*Diprotodon*, *Nototherium*, *Phascolonus*, *Phascolomys*, *Macropus*, *Sthenurus*, *Bettongia*, *Perameles*, *Thalacomys*, *Dasyurus*, *Thylacinus*, and *Thylacoleo*. Scott and Lord have published records in Tasmania of *Diprotodon*, *Nototherium*, *Palorchestes*, *Sthenurus*, and *Macropus*.

This wealth of widely spread fauna surely demonstrates that our marsupials have been long in the land. Bensley (1903, pp. 206-207) expressed the view that the lowest estimate of the duration of the evolution of the Australian marsupials is still much too large, and he thought it unlikely that "the marsupial radiation could have begun until well on into the middle of the Tertiary period." But Bensley's elaborate review dealt mainly with existing species, and he does not appear to have fully appreciated the wealth and divergencies of our fossil forms. It seems far more probable that Osgood is correct when he says (1921, p. 131) "the view that all living families of marsupials were well differentiated early in the Tertiary seems to be well founded." In the clash of conflicting views as to the age of marsupials in Australia, it is difficult to obtain a proper perspective. No one, however, can carefully examine a large and comprehensive collection of our fossils without recognising that they represent an assemblage resulting from a lengthy process of evolution, which, in the great majority of genera, cannot be associated with any forms yet found outside the Australian regions.

The many changes that have taken place in land masses of the Australian

region since Cretaceous times, as outlined by Jensen and others, cannot be dealt with here, but it is evident that a variety of environments was available for the evolution of our marsupials from remote ancestors which were northern in origin.

**Myrmecoboides.**—Special interest has been attached to the presence of *Myrmecoboides*, with supposed peramelid affinities in the Paleocene of Fort Union, North America. Gidley's notable work on this fragment (an incomplete ramus of a lower jaw) perforce deals mainly with dental characters. The resemblances to *Myrmecobius* are very suggestive, but are not conclusive, and may be the result of convergence. Gidley (1915) notes that the name *Myrmecoboides* was given on account of its likeness to *Myrmecobius* rather than as a positive assumption of real relationship. He does not accept Osborn's or Bensley's view concerning the phylogeny of modern families of marsupials, and assumes "a vastly more ancient origin" than has hitherto been held for them. He states: "In fact, it seems reasonable to assume that at present nothing is definitely known regarding the origin of several of the living families of marsupials, including probably all the diprotodonts, because they are not represented in our collections from beds older than the Pleistocene, and that in the lower fossils we have only an incomplete and indefinite history of the origin and development of a part only of the polyprotodonts" (p. 401).

Osgood (1921, p. 140) states: "The hypothesis can scarcely be avoided that, provided *Myrmecoboides* is a marsupial, it may well be ancestral to the cænolestids."

**South American Fossils.**—The Sparassodontia of Ameghino from the Miocene of Patagonia are placed by W. T. Sinclair in the Family Thylacinidæ. But it is significant that in *Borhyaena* the canine is actually replaced and in *Prothylacinus* the canine and two premolars are replaced. This marked tendency to a diphyodont dentition is unparalleled in Australian forms. Palatal vacuities and epipubic bones are lacking, and R. Lydekker, in 1907, in analysing these and other features, expressed the opinion that the Patagonian fossils were Creodonts and not marsupials. W. K. Gregory (1910, p. 207) states that these fossils show "a remarkable series of resemblances in general proportions and dental characters to some of the Creodonts among Placentals. . . . The family Thylacinidæ is thus seen to be a specialized offshoot either of very primitive Dasyuridæ or more directly from the Didelphiidæ."

Gidley (1915, p. 401) points out that in the Miocene the Thylacinidæ had reached almost their present state of specialization. They certainly do not represent a primitive type suggesting an ancestral source for Australian forms. Tate Regan (1914) adversely criticises the suggested relationship between the two groups.

It is by no means improbable that the resemblances between the Patagonian fossils and *Thylacinus* are due to convergence. But even if the lineal relationship were definitely proved, which Sinclair does not suggest, the South American origin of our Diprotodontia would still be without a satisfactory basis.

The position of the remarkable American marsupial *Cænolestes* has been

discussed in great detail by several authors, and it has been placed in no less than three sub-orders. Whilst many of its characters suggest that it may represent a prototypical generalized form, from the ancestors of which diprotodonts may have been derived, it seems to the writer that far weightier evidence is required before we associate the varied and manifold Diprotodontia of Australia with this marsupial from the Andes.

Among the many interesting points raised by Osgood in his elaborate memoir on *Cænolestes* is the fossil evidence that the diprotodont dentition of the cænolestid group goes back far in geological time, "perhaps in the Mesozoic," as the didelphids and cænolestids were already well distinguished in the Patagonian Miocene (Osgood, 1921, p. 129). Among his conclusions he states: "The ancestor of the cænolestids was probably a northern form which had already separated from the generalized polyprotodont stock. . . . The North American ancestor of the cænolestids possibly extended throughout Holarctica and therefore may also have given rise to the Australian diprotodonts. This assumes that the main lines of divergence between Diprotodonts and Polyprotodonts were established in the north prior to the Australian and South American radiations. Hence an Antaretic land connection is not necessary to explain the resemblances between American and Australian marsupials" (p. 151).

W. K. Gregory (1910) points out that the pes is "entirely elcuthero-dactylous," and he is inclined to regard *Cænolestes* and its allies as an independent sub-order, an offshoot of primitive Polyprotodonts, which has paralleled the Diprotodonts in certain characters of the dentition" (p. 211).

Gidley (1915, p. 401) states that the Cænolestidæ "more probably belongs with the Polyprotodonts."

In his analyses of the affinities of *Cænolestes* in 1911, R. Broom considers that it "was much more nearly allied to the American Polyprotodonts than to the Australian Diprotodonts" (p. 315).

Assuming that Wood Jones's argument for the special primitiveness of syndactylism is correct, the fact that modern cænolestids are diadactyl is an important point. It is also significant that a diprotodont dentition has independently appeared in several orders. It seems most probable that the resemblances between cænolestids and Australian diprotodonts are mainly due to convergence, but partly patterned by remote ancestral inheritance. There is now manifold evidence for the phenomena of convergence in obviously unrelated orders; it may be urged, *a fortiori*, that convergence is still more likely to appear in groups distantly related owing to the working out of similar ancestral potentialities.

Gregory (1910, pp. 212-213) writes: "Marsupials in general, and especially South American families of many orders, seem to abound in examples of homoplastic and convergent resemblances to animals of other orders."

Ameghino, who has described so many of the South American fossils, necessarily relies mainly on dental characters. In his phylogenetic diagram of

diprotodonts (1903, p. 188) he derives his *Hypsiptymnoidea* ("diprotodontes *australianos*") from the ancestral Garzonidæ through the primitive Cænolestidæ. After referring to the affinities of northern forms of Multituberculates with Patagonian fossils, he says: "Además, la transición entre los paucituberculados de la Argentina (Epanorthidæ, Cænolestidæ), y los diprotodontes actuales de Australia, es igualmente tan completa, que ya no es discutible la conclusión de que todos en conjunto constituyen un solo gran grupo." But the unitary grouping of the Cænolestidæ and Diprotodontia is not accepted by many authorities, and it seems a colossal assumption to derive the varied families and genera represented in Australia from the American species.

**Wynyardia.**—Baldwin Spencer's description of *Wynyardia bassiana* (1900) forms a notable contribution to the records of Australian vertebrate fossils. These remains, which have been attributed to the Eocene, were unaccompanied by teeth, but the describer instituted a large number of comparisons, based on available characters, and came to the conclusion that *Wynyardia* represented a form distinct from present marsupials, but allied to both existing Polyprotodontia and Diprotodontia. Osgood (1921) has criticised the diagnostic value of many of the characters set out by Spencer in his comprehensive analysis, but, whilst agreeing with the view that *Wynyardia* combines many features of the two groups, classifies it with the diprotodonts and makes it the type of a new family—*Wynyardiidae*. He then compares this fossil with *Cænolestes*, as suggested by Gregory in 1910.

It appears to the writer that *Wynyardia* has no real relationship with *Cænolestes*, and that the differences are far more marked than the eight resemblances noted by Osgood (p. 139). The proportions of the nasals and the slope of the sutures between premaxillæ and maxillæ, mentioned by him, are most variable in modern marsupials of the same genus, and are of no real diagnostic value.

Among the many distinctions between *Wynyardia* and *Cænolestes* which can be noted by comparing the two forms, I have drawn up the following, which seem to be significant:—

The squamosal is extremely large ("a very remarkable feature"—Spencer) in the Tasmanian fossil, and excludes the alisphenoid from union with the parietal, whilst in *Cænolestes* the alisphenoid has a wide union with the upper element.

The zygomata are massive in *Wynyardia* and set relatively high; in *Cænolestes* they are slender and are set low.

The lachrymal in *Wynyardia* is so well developed that it actually prevents contact between the maxillary and nasal bones, being in striking contrast to the American form.

The occipital regions in the two fossils are quite unlike.

So far as can be judged from the mandibular fragment of *Wynyardia*, it is utterly dissimilar from the lower jaw of *Cænolestes*.

The tibia of *Wynyardia* is of a very different type, and the fibula "is a complete separate bone."

It should be stated that Osgood recognised that his comparison between the two forms was "rather unsatisfactory as a basis for positive conclusions."

Osgood also compares *Wynyardia* with extinct American forms, *Palæothentes* and *Abderites*, allied to *Cænolestes*. One of the most remarkable features of the Tasmanian fossil is the presence in the incomplete ramus of the lower jaw of "a deep depression across the upper surface, which must apparently have been situated in the area occupied by the molar series. It extends in a slanting direction from side to side across the jaw, and its smooth, rounded floor-surface and margins show clearly that it is not a mere break in the jaw. With this is associated a swelling on the internal face. . . ." (Spencer, p. 784). The describer suggests that it may have been associated with the presence of a large sectorial tooth in the molar or premolar series such as is developed in *Abderites*. Gregory (1910, p. 215) instances an alveolar groove in Ameghino's *Garzonina minima*, and Osgood, in 1921, writes that the structure of the lower sectorial tooth in *Abderites* "seems closely comparable to the condition in *Wynyardia*." When Ameghino's figures of *Abderites meridionalis* and of *Garzonina minima* are consulted, it seems to the writer that there is no evidence whatever of relationship. In these American fossils we see no sign of the remarkable contours figured for *Wynyardia*. Assuming that the depression represents diastemata between molar series and incisors, then there is no similarity between the two groups of fossils. Should this smooth transverse furrow be interpreted as representing the site of a large sectorial tooth that had been accidentally lost long before the death of the animal, then comparisons for this special feature might quite as well be instituted between *Hypsiptymnodon* or even *Phalanger*, present Australian forms with prominent oblique premolars. To suggest a theory of relationship on the possible shape of a tooth that is not even represented by an alveolus is, however, far beyond the scope of this paper.

In the light of our present knowledge, there appears to be no valid reason for suggesting that *Wynyardia bassiana* is related to the cænolestids of South America.

Two fossils from eastern Australia are significant because they demonstrate combinations of characters. *Burramys parvus* from Taralga, N.S.W., described by R. Broom in 1895, has a large grooved premolar, and is probably an annectant form between the Macropodidae and Phalangeridae. *Triclis oscillans*, from King's Creek, Darling Downs, Queensland, has somewhat similar characters, and was compared by De Vis (1888) to the existing *Hypsiptymnodon*.

In 1916 W. D. Matthew described, under the name of *Eodelphis browni*, a primitive opossum from the upper Cretaceous of Alberta. Referring to this form, Gregory (1920, p. 156), in reviewing the early polyprotodont marsupials, says: "The more primitive members (*Eodelphis*) seem to be directly ancestral to

the modern Didelphiidæ of North and South America, and were also probably related to the Upper Cretaceous European and Asiatic polyprotodonts that were ancestral to the later Australian members of this group."

#### BRIEF NOTES ON THE NON-MARSUPIAL FAUNA.

**Monotremes.**—The absence of monotremes from South America and their special development in Australia is evidence of their northern origin, probably in pre-Tertiary times. The development of *Zaglossus* and *Prozaglossus* (Kerbert, 1913) in Papua is significant. Pliocene monotremes have been recorded by W. S. Dun (1895) from New South Wales. Species of *Zaglossus* have also been recorded by L. Glauert from West Australian deposits, and by Scott and Lord from Tasmania. Two genera are represented in Darling Downs deposits.

**Rodentia.**—The evidence of other mammals is distinctly favourable to the hypothesis of lengthy and extensive northern land connections. In 1916 the writer remarked on the significance of about fifty autochthonous species of rodents in Australia and Tasmania. Since then the list has considerably increased. So far as I am aware, no alternative to a northern origin of the ancestors of these rodents has ever been suggested.

**Reptilia.**—With regard to the reptilian fauna, Thomas Barbour, in his valuable study of the Zoogeography of the East Indian Islands (1912) states: "The remarkable development of Ophidia proteroglypha in Australia can hardly be explained by assuming that they came from South America." He holds, on the contrary, that they originated in Asia and spread through Australia to South America (p. 155). He refers elsewhere to the strong Australian and perhaps a Papuan tinge in the fauna of Timor, instancing *Chelodina* and *Liasis*.

If we eliminate such genera as *Typhlops* and *Natrix*, which are cosmopolitan and presumably palæogenic forms, we find that the affinities of our ophidian fauna are certainly not with America. There are no true pythons in America, and our genera of constricting snakes are evidently northern in origin. Of the *Acrochordinae*, *Acrochordus* and *Chersydrus* are northern, and this also applies to the genera of *Homalopsinae* and to *Dendrophis*. Compared with the rich development of Elapine snakes in Asia, Africa, and Australia, this group is sparsely represented in America. The *Hydrophiinae* have special means of distribution, but if they are entitled to consideration they tell the same story. The paramount affinities of the Australian snakes as a whole are undeniably northern.

Many species of Ophidia, Lacertilia, and Chelonia are common to North Queensland and Papua.

Of the Lacertilia, the Geckonidæ and Scincidæ are so cosmopolitan that no special significance can be attached to their distribution, although Australia has such distinctive genera as *Nephrurus* and *Trachysaurus*, to mention but two. The Pygopodidæ are confined to Australia and Papua. The Agamidæ and

Varanidæ are African, Asiatic, and Australian in range. There are no Iguanidæ in our region. The lacertilian fauna affords no evidence whatever for an American invasion, and its affinities are decidedly northern.

**Amphibia.**—Much has been made of the presence of Cystignathidæ in America and in Australia, but it seems exceedingly doubtful whether the many genera of frogs placed in this family in these regions constitute a natural assemblage. Gadow writes: "The numerous genera not only run into each other, but also get entangled with those of other families. In fact the whole family is ill defined." (1909, p. 209). Amongst the amphibians the phenomena of convergence are very well known.

Van Kampen has pointed out that many Indian forms of Amphibia must have reached Papua by ancient land connections (1909).

**Fishes.**—The evidence of certain fresh-water fishes (Galaxiidæ and Aplochitonidæ) found in Australia, New Zealand, and South America has been repeatedly stressed by the exponents of the Antarctic connection. Tate Regan, however, insists that these are of marine origin (1914) and A. R. McCulloch (1915) actually discovered young specimens of *Galaxias attenuatus* making their way from the coast into fresh water. Regan (*loc. cit.*) points out that the only true fresh-water fishes common to these regions are the Osteoglossidæ, and that our well-known representative of this ancient group (the Barramundi, *Scelopropages leichhardti*) has greater affinities with Asiatic forms. He concludes that "neither marine nor fresh-water fishes support the theory that the Antarctic continent connected America with Australia during the Tertiary Period." (p. 41).

Max Weber and de Beaufort have found an Australian element in the fresh-water fishes of the Aru Islands and Waigen, and an interesting summary of their views appears in "The Zoology of the Indo-Australian Archipelago" (1923.)

**Flora.**—The present endemic nature of the great bulk of the Australian fauna is borne out by the testimony of the flora. The "original Australian flora" (to use Maiden's term) is the dominant group on the western side, where it apparently developed. On the east, however, the Austro-Malayan element is the more prominent, and one may reasonably suggest that only an unfavourable environment prevented its extension into temperate regions towards the south and eremian regions to the west. There appears to be no absolute need to postulate a land bridge, suitable for emigrating mammals, with South America to account for the third, or so-called Antarctic element.

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The writer is in no way competent to comment on the geological evidence, but, judging from R. N. R. Brown's review of the problems of Antarctica (1923), further exploration is needed before the relationships of the eastern and western portions can be made clear. W. N. Benson, in his able study of Palæozoic and Mesozoic seas in Australasia, gives strong evidence of the land connection of Australasia with Antarctica and South America at the close of Mesozoic

times, but it must be noted that, at the same time, there were land connections to the north and north-east linking Australia with the remains of the ancient continent called *Æquinoctia*, by E. C. Abendanon (1919, p. 577). Similar northern extensions are a salient feature of Hedley's map, published in 1909 (p. 333). The probable extent of this northern continental mass, as it may have existed in early Mesozoic times, is shown by A. B. Walkom (1918, text-figure 2, p. 105). The shallow submarine plateau connecting Australia with Papua, the Aru, and some other islands is called "the Sahul flat" by Molengraaf.

There is some diversity of opinion as to the age of the connections denoted by the great shelves in what Molengraaf calls "the Australasian Mediterranean" (1921), and it is not improbable on zoological evidence that the first connections may have been long anterior to the relatively recent variations, which may have been indirectly effected by glacial and interglacial periods.

Valuable references to the views of authorities on the relationships of the Asiatic and Australian faunas are given in "The Zoology of the Indo-Australian Archipelago" (1923); whilst Chilton (1909) gives an interesting summary of the relationships of circum-austral forms from the New Zealand standpoint.

The assumption of a continent in the Antarctic in early Tertiary times, in order to account for related elements in the faunas and floras of South America, Australia, New Zealand, various Pacific Islands, Madagascar, and South Africa, has proved a veritable Pandora's box to biologists. In order to explain many of the difficulties raised, it is suggested that this circumpolar area had radiating land bridges, inconstant in direction and dimension, apparently reaching out on the one hand to deposit certain types in Pacific archipelagoes; elsewhere stretching to Madagascar to transfer iguanas; extending to New Zealand to allow other forms to gain new land; and independently reaching Tasmania to enable the ancestors of our marsupials to complete a trans-polar journey and find a congenial refuge.

The presence of more extensive land areas in the Antarctic in Mesozoic times is apparently demonstrated, but it seems improbable that these areas were faunal land bridges for vertebrates. On the other hand, the presence of "ancient continental" islands to the north-west, as shown by Russel Wallace in "Island Life" and the "Geographical Distribution of Animals," is undoubted. That the evidence of these "ancient continental" islands is incomplete is doubtless due to partial or entire submergence. In this connection it is interesting to note that Weber and Beaufort (1912) in their analysis of the fresh-water fishes of Timor found that this fish fauna was "almost totally composed of immigrants from the sea," the inference being that the island had been largely submerged in Tertiary times.

Possibly fossils from the Austro-Malayan-Asiatic regions will one day be forthcoming to strengthen the view that our marsupials had a northern origin probably before "Wallace's Line" had significance as a partial barrier. But even on existing evidence, it seems to the writer that the alternative route of Antarctic land bridges involves us in far greater difficulties and anomalies.

### CONCLUSIONS.

A fundamental consideration regarding the origin of Australian marsupials is the undoubted fact that the group was once widely distributed in Holarctic or northern regions.

A second consideration is the present-day knowledge that North Australia and Papua maintain a wealth of diverse marsupial genera, the significance of which could not be realised in earlier discussions.

A third consideration is the demonstration that our extinct marsupial fauna was even more distinctly Australian than that of to-day; the evolution of the group has largely taken place here.

A fourth consideration is that the differences between *Wynyardia bassiana*, our oldest marsupial fossil, and the South American Cænolestids far outweigh the resemblances.

A fifth consideration is that the most characteristic group of Australian marsupials, the Diprotodontia, has little or nothing in common with South American forms; the slight resemblance between *Cænolestes* and our diprotodonts is probably due to convergence.

A sixth consideration is the demonstration by Osgood that "didelphids and cænolestids were already well distinguished in the Patagonian Miocene," and that "the view that all the living families of marsupials were well differentiated early in the Tertiary seems to be well founded" (p. 131).

A seventh consideration is the rich development of the primitive family Peramelidæ in the Austro-Malayan region.

An eighth consideration is that distinctive syndactylism is a special Australian feature; Wood Jones has analysed the alternative values of dental and pedal characters, demonstrating that syndactylism is the more primitive feature.

These and other considerations are supported by evidence, briefly outlined in this paper, dealing with the probable relationships of several non-marsupial groups (monotremes, rodents, etc.) of the Australian fauna, and the work of zoogeographers on the Indo-Australian Archipelago is considered of special importance.

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